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ACCUMULATION OF MERCURY BY PLANKTON AND BENTHIC INVERTEBRATES IN RIVERINE LAKES OF NORTHERN MANITOBA (CANADA): IMPORTANCE OF REGIONALLY AND SEASONALLY VARYING ENVIRONMENTAL FACTORS

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Accumulation of Mercury by Plankton and Benthic Invertebrates in Riverine Lakes of Northern Manitoba (Canada): Importance of Regionally and Seasonally Varying Environmental Factors

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Mercury (Hg) concentrations in plankton and benthic invertebrates from riverine lakes of northern Manitoba were generally found to be unrelated, or inversely related, to inorganic and methyl mercury levels and Hg methylation rates in their habitats but were strongly dependent on environmental factors. The relationships suggest that the uptake of Hg by these organisms was controlled largely by suspended and sedimentary Hg-binding substances such as FeOOH, MnOOH, organic matter, sulfides, and clay. The sole exception was midsummer phytoplankton, whose Hg content was a function of Hg levels in local sediments, probably because interference by suspended detritus was minimal; during the spring flood, such interference had a predominant effect. Aeration of lake water by fluvial currents probably enhances the availability of Hg to plankton by promoting decomposition of organic matter and sulfides but decreases the availability of Hg to some benthic animals by causing MnOOH precipitation. FeOOH apparently limits Hg uptake by chironomid larvae but MnOOH limits Hg uptake by oligochaetes, nematodes, and pelecypods, suggesting preferential uptake of certain forms of Hg by particular biological and mineral species. Decreases in temperature may also retard Hg uptake by benthos. Biodilution has no significant effect on Hg accumulation by benthos or plankton.

La teneur en mercure (Hg) chez les invertébrés planctoniques et benthiques de lacs situés dans le nord du Manitoba n'était pas liée en général, ou était inversement liée, à la teneur en mercure inorganique et en méthylmercure, et au taux de méthylation du Hg dans leur habitat, mais elle était fortement dépendante de facteurs environnementaux. Le rapport semble indiquer que la fixation de Hg par ces organismes était régie en grande partie par des substances sédimentaires et en suspension fixant le Hg comme le FeOOH, le MnOOH, la matière organique, les sulfures et l'argile. La seule exception était le phytoplancton du milieu de l'été dont la teneur en Hg était fonction de la teneur en Hg dans les sédiments locaux en raison sans doute du peu d'interférence que présentaient les débris en suspension; pendant la crue printanière, cette interférence avait un effet prédominant. L'aération de l'eau du lac par les courants fluviaux augmente probablement la disponibilité du Hg pour le plancton en favorisant la décomposition de la matière organique et des sulfures mais diminue la disponibilité du Hg pour certains animaux benthiques en provoquant la précipitation du MnOOH. Il semble que le FeOOH limite la fixation de Hg par les larves de chironomidés mais le MnOOH limite la fixation de Hg par les oligochètes, les nématodes et les pélécypodes, ce qui semble indiquer une fixation préférentielle de certaines formes de Hg par des espèces biologiques et minérales particulières. Des baisses de température peuvent aussi retarder la fixation du Hg par le benthos. La biodilution n'a aucun effet important sur l'accumulation de Hg par le benthos ou le plancton.

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A previous paper (Jackson 1988b) treated the biogeochemistry of mercury (Hg), especially the production of methyl mercury (CH_3Hg^+), in sediments and water of lakes along the Churchill River diversion route in northern Manitoba, with emphasis on effects of environmental alteration caused by recent hydroelectric development. In the present paper, the accumulation of Hg by plankton and benthic invertebrates in these lakes is examined. The purpose of the study was to investigate effects of environmental factors in general, and the impact of reservoir creation in particular, on Hg levels in planktonic and benthic organisms.

Hg concentrations in the plankton and benthos of lakes in northern Manitoba have also been studied by Bodaly et al. (1987) and W. F. Warwick (National Hydrology Research Institute, 11 Innovation Blvd., Saskatoon, Sask. S7N 3H5, unpubl. data).

Field Area, Materials, and Methods

A full description of the field area, together with a detailed treatment of the collection and analysis of sediment and water samples, has been given elsewhere (Jackson 1988b). Briefly, the samples for the present study were taken from Granville Lake, Southern Indian Lake, (South Bay and a shallow cove of Long Bay (= Wupaw Bay)), and selected lakes of the "Notigi

Reservoir" complex (Rat Lake, Central Mynarski Lake, and the east and west basins of Notigi Lake) (Jackson 1988b, fig. 1).

Granville Lake (the "control" region) has not been altered by the Churchill River diversion, while the other lakes have been affected to different degrees by the impoundment and rerouting of river water and resultant flooding of adjacent land. The impact of flooding on the aquatic environments, including the subsequent increase in rates of CH_3Hg^+ production in sediments and CH_3Hg^+ accumulation by fish, has tended to increase in the order Granville Lake < Southern Indian Lake < Notigi Reservoir lakes (Bodaly et al. 1984; McGregor 1980; Jackson 1988b). Superimposed on these general effects of recent flooding are the following geographical variations in the lacustrine environments (Jackson 1988b): (1) "main-stream" regions are vigorously flushed by river water flowing through them, while "backwater" regions are quieter and less rapidly flushed; therefore, backwater environments are influenced to a greater extent by local drainage and accumulate higher concentrations of allochthonous organic matter derived from local forest soils and muskeg (Jackson and Hecky 1980); (2) South Bay is bordered by Pleistocene silty clay deposits which are undergoing erosion, causing locally elevated turbidity that decreases gradationally in the order South Bay > Rat Lake > Notigi Lake; (3) Granville Lake and the west basin of Notigi Lake have certain anomalies in common, such as high primary productivity (Bodaly et al. 1987; Jackson 1988b), the presence of manganese nodules, and sediments with elevated manganese/iron (Mn/Fe) ratios and low clay concentrations, which set them apart from the other regions and suggest exceptionally vigorous mixing, agitation, and aeration (Jackson 1988b).

Samples of >10 μm plankton were taken during 23–25 June (the time of the spring flood) and 11–13 August 1981. Integrated water samples were collected with a flexible plastic tube lowered to about twice the depth of visibility as determined with a Secchi disk, and the plankton was filtered out by passing known volumes of this water through a 10-μm net designed to trap phytoplankton (except for the tiny "picoplankton species (Stockner and Antia 1986)) together with zooplankton. The plankton samples were freeze-dried and stored for chemical analysis.

Benthic macroinvertebrates (see also W. F. Warwick, unpubl. data) were sampled during 23–25 June 1981. Bottom sediments were collected with an Ekman dredge 15.2 × 15.2 cm in cross section, and the fauna was isolated by screening the sediment through a 200-μm net. The different taxonomic types were then separated, identified, weighed, frozen at −40°C, and stored for chemical analysis. Before being frozen, chironomid larvae were bathed in water, with daily changes of water, for 2–3 d without food to void their gut contents. This procedure was not feasible with the other types of invertebrates.

All biological specimens were wet-ashed and analyzed for total Hg by flameless atomic absorption spectrophotometry (Jackson 1988b). The plankton samples were digested with H_2SO_4, HNO_3, and $KMnO_4$ (Armstrong and the Uthe 1971), and the benthic invertebrates were digested with H_2SO_4, HNO_3, HCl, $KMnO_4$, and $K_2S_2O_8$ (Mercury Sampling and Analysis Review Committee 1977). Hg data for benthic invertebrates were computed on the basis of fresh weight and data for plankton on the basis of dry weight. Replicate analyses were performed on three of the benthic invertebrate (chironomid) samples. Owing to the small sample sizes, however, only single analyses could be performed on the other samples.

Samples of zooplankton were not available for analysis, but Hg data for >73 μm zooplankton collected from the same sampling areas by other workers were obtained from the literature (Bodaly et al. 1987). The zooplankton samples were collected with horizontally towed nets during 18–20 June and 17–19 August 1981 and were stored in the frozen state before being analyzed for Hg. The data were computed on the basis of dry weight.

The Hg data for the planktonic and benthic organisms were correlated with various analytical data representing sediments and water collected from the same sampling sites in 1981 and 1983. The data for the sediment and water samples, an account of the methods used for collecting and analyzing these samples, and definitions of the biogeochemical parameters employed have been published elsewhere (Jackson 1988b). The following definitions are explained in full in Jackson (1988b) but are briefly repeated here for the reader's convenience: (1) the "available inorganic Hg" fraction of bottom sediment = all Hg extracted with N_2-purged 0.5 M $CaCl_2$; (2) the sediment's "total organic Hg" fraction = Hg extracted by the procedure used for extracting CH_3Hg^+ and subsequently determined as total Hg rather than CH_3Hg^+ as such; and (3) the sediment's "Hg methylating capability" (or relative rate of methylation) = the quantity of CH_3Hg^+ generated by 10 g of sediment dispersed in 20 mL of 10 μM $HgCl_2$ solution when incubated for 10 d at 25°C under an atmosphere of N_2.

Relationships between data were assessed by regression analysis. Correlation coefficients (r) and significance probabilities (P) were computed for linear, log–log, semi-log, parabolic, and hyperbolic regression lines, and the regression formulas yielding the highest r and P values were selected as the nearest approximations of the trends. A relationship was defined as "significant" if $P \leq 0.05$.

Results and Discussion

Hg levels in plankton and benthic invertebrates varied systematically as functions of certain environmental parameters; but, except in the case of >10 μm plankton sampled in August, they showed no significant relationship — or, surprisingly, showed an inverse relationship — with the total Hg, particulate Hg, and CH_3Hg^+ content of the water and the total Hg, CH_3Hg^+, and available inorganic Hg content and Hg methylating capability of the bottom sediment. Thus, with the exception of >10 μm plankton in August, Hg concentrations in plankton and benthos were entirely, or almost entirely, independent of the environmental effects of hydroelectric development. This is remarkable, because flooding due to hydroelectric development has caused a pronounced increase in the Hg methylation rates and concentrations of CH_3Hg^+ and total Hg in sediments (Jackson 1987, 1988b; Ramsey and Ramlal 1987) and the Hg content of fish species such as walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) (McGregor 1980; Bodaly et al. 1984).

Hg in Plankton

Plankton sampled in June

The Hg content of >10 μm plankton collected in June was highest in the rapidly flushed, well-aerated mainstream regions and lowest in the relatively stagnant backwater regions and appeared to be entirely unaffected by postimpoundment flooding due to hydroelectric development (Table 1). The plankton

TABLE 1. Hg content of >10 μm and >73 μm plankton collected in June and August 1981. The data for >73 μm plankton were taken from Bodaly et al. (1987) and recalculated. n.d. = no data.

	Hg concentration (nmol/g dry wt.)			
	June		August	
Sampling site	>10 μm	>73 μm	>10 μm	>73 μm
Granville Lake	5.48	0.10	3.2	6.13
East Mynarski Lake	n.d.	0.19	n.d.	1.9
Southern Indian Lake				
Long Bay (shallow cove)	5.33	n.d.	6.28	n.d.
Long Bay (main basin)	n.d.	0.17	n.d.	n.d.
South Bay	10.5	0.50	3.1	0.1
Notigi Reservoir				
Rat Lake	n.d.	n.d.	1.6	n.d.
West Mynarski Lake	n.d.	0.55	n.d.	1.4
Central Mynarski Lake	4.2	0.25	n.d.	0.2
Notigi Lake (west basin)	6.43	0.50	10.3	4.2
Notigi Lake (east basin)	n.d.	0.28	7.03	4.4

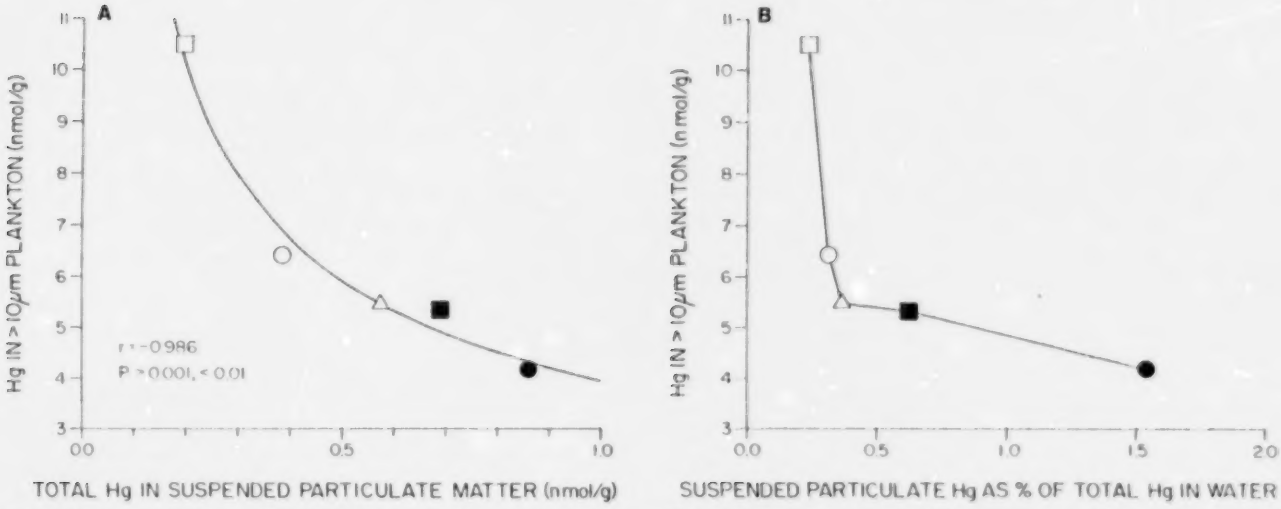
A
B
Hg IN >10μm PLANKTON (nmol/g)
r = -0.986
P > 0.001, < 0.01
TOTAL Hg IN SUSPENDED PARTICULATE MATTER (nmol/g)
SUSPENDED PARTICULATE Hg AS % OF TOTAL Hg IN WATER

FIG. 1. Relationship between Hg in >10 μm plankton collected in June 1981 and the total suspended Hg expressed as (A) concentration per unit weight of suspended matter and (B) percentage of the total Hg in the water. Solid symbols, backwater sites; open symbols, mainstream sites. △, Granville Lake; □ or ■, Southern Indian Lake; ○ or ●, Notigi Reservoir lakes.

from South Bay in Southern Indian Lake was richest in Hg, the plankton from Central Mynarski Lake in Notigi Reservoir was poorest in Hg, and plankton from other Southern Indian Lake and Notigi Reservoir sites and from Granville Lake was intermediate (Table 1). This was unexpected because the results of previous research on the effects of reservoir creation on the bioavailability and bioaccumulation of Hg in lakes of northern Manitoba (Jackson 1987, 1988b; Bodaly et al. 1984) suggest that the Hg content of the plankton ought to increase in the order Granville Lake < Southern Indian Lake < Notigi Reservoir lakes. Nevertheless, these findings were corroborated by the Hg data for the >73 μm plankton (Table 1). Thus, >10 μm and >73 gm plankton samples collected and analyzed independently by different workers indicated comparable geographic patterns of variation. However, the distinction between mainstream and backwater samples was less clear-cut in the >73 μm plankton (Table 1). The >73 μm plankton samples with the lowest Hg content came from the "control" site on Granville Lake, which has a mainstream environment.

Unexpectedly, the concentration of Hg in >10 μm plankton gave a significant *negative* correlation with the concentration of Hg in the suspended particulate matter in the ambient water (Fig. 1A). Essentially the same result was obtained if the abundance of particulate Hg was expressed as percentage of the total Hg burden of the water (Fig. 1B) or as quantity of particulate Hg per unit volume of water ($r = -0.883$; $0.05 > P > 0.02$). Similarly, the Hg content of the plankton was inversely related to the sulfide content of the bottom sediment (Fig. 2). Hg levels in the >10 μm plankton also gave statistically insignificant negative correlations with CH_3Hg^+ levels in bottom sediment and water, with total Hg and $CaCl_2$-extractable Hg concentrations in sediments, and with the sediment's relative rate of CH_3Hg^+ production as represented by its "Hg methylating capability" and gave an almost totally insignificant positive correlation with the total Hg content of the water (Table 2).

A striking feature of the curves in Fig. 1A, 1B, and 2 is the distinct separation of data for mainstream and backwater sites. Another noteworthy observation is that the curves in Fig. 1B and 2 are essentially hyperbolic.

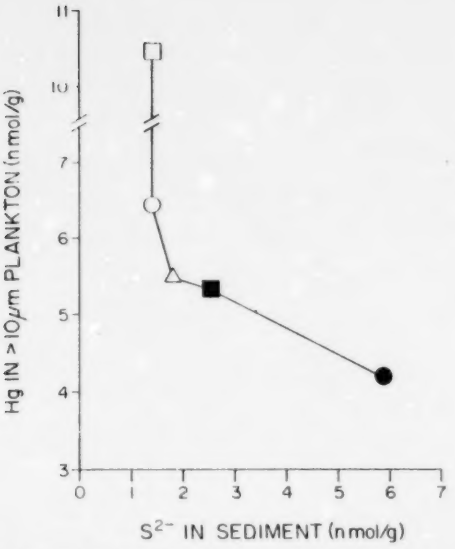

FIG. 2. Relationship between the Hg content of >10 μm plankton collected in June 1981 and the nonvolatile sulfide (S^{2-}) content of the bottom sediment. Explanation of symbols same as in Fig. 1.

In addition, the Hg content of >10 μm plankton decreased logarithmically with increasing concentration of organic matter in the sediment (Fig. 3A). A plot of Hg in >73 μm plankton against the organic carbon (C) content of the sediment gave similar results (Fig. 3B), except that the plot is split into two separate curves differing greatly in slope and diverging widely, although both are logarithmic; samples from the Notigi Reservoir lakes, which have been more extensively altered by post-impoundment flooding and whose sediments are richer in organic C, show a much more gradual decline in the Hg content of >73 μm plankton than do samples from Southern Indian Lake and Granville Lake, which were altered to a considerably lesser extent or (in the case of Granville Lake) not at all, and whose sediments have lower concentrations of organic C.

Hg levels in >10 μm plankton showed a weak inverse relationship with the concentrations of organic C ($r = -0.849$; $0.1 > P > 0.05$) and total nitrogen (N) ($r = -0.825$; $0.1 > P > 0.05$) in the bottom sediments but gave a very significant *positive* correlation with the organic C/N ratio of the sediment (Fig. 4A). Hg levels in >73 μm plankton gave similar results (Fig. 4B) except that in South Bay, which has an anomalously heavy load of suspended clay and silt, the Hg content of the plankton is much lower than the value predicted by the regression formula for the other data, causing the curve to level off abruptly.

The results presented in Tables 1 and 2 and Fig. 1–4 suggest that Hg uptake by >10 μm and >73 μm plankton sampled in June was regulated principally by the bioavailability of Hg in the environment, not by the total abundance of either inorganic (nonmethyl) Hg or CH_3Hg^+. According to this interpretation, the availability of Hg to plankton decreased with increasing concentrations of suspended and sedimentary organic matter and sulfides owing to the tendency of these substances to bind Hg strongly. Both organic C and sulfide are most abundant in poorly flushed backwater environments because organic matter derived from the surrounding heavily forested and muskeg-covered land accumulates there (Jackson 1988b). They are least abundant in mainstream environments, presumably because of rapid flushing and dilution, as well as accelerated decomposition by oxidation. Consequently, in backwater regions the amount of Hg fixed in biologically unavailable forms by nonliving particulate matter is probably higher in proportion to the amount of Hg taken up by plankton than is the case in mainstream regions. We may tentatively conclude that the observed geographical variations in the Hg content of the plankton were determined primarily by the environmentally dependent variations in the outcome of this partitioning process.

This interpretation is supported by the following facts: (1) mainstream bottom sediments had the greatest abundance of $CaCl_2$-extractable Hg per unit amount of total Hg, indicating the highest degree of Hg availability, even though Hg in plankton did not correlate with $CaCl_2$-extractable Hg; and (2) the $NH_2OH{\cdot}HCl$-extractable oxides of mainstream sediments had the highest Mn/Fe ratios, suggesting that the most highly oxidizing conditions occurred in the mainstream zone (Jackson 1987, 1988b). The positive correlation between the Hg content of >10 μm and >73 μm plankton and the organic C/N ratio of bottom sediment is another reflection of this phenomenon. The more intense the decomposition of organic matter, the higher the C/N ratio of the residue because of preferential decomposition of labile nitrogenous organic compounds (Kemp 1971). Consequently, the organic C/N ratio of the sediment as well as the Hg content of plankton tends to be highest in the vigorously agitated, well-aerated mainstream environments. The anomalous results obtained for South Bay (Fig. 4B) may well signify that the exceptionally large quantity of suspended clay and silt at that site suppresses the uptake of Hg by zooplankton or gives rise to an aberrantly high organic C/N ratio in the sediment, owing, perhaps, to some process such as preferential adsorption of the more C-rich, higher molecular weight humic fractions by the clay. Site-dependent differences in the species composition of the plankton communities could conceivably have played a role as well, but the information required to assess this possibility is lacking.

Theoretically, high C/N ratios could also represent high ratios of allochthonous (terrestrial) to autochthonous (aquatic) organic matter (Hutchinson 1957; Jackson 1988b), but this is unlikely in the present case. If this were the correct explanation, backwater regions and the environments most strongly affected by flooding would have given the highest C/N ratios.

Variations in the total biomass of the aquatic community leading to different degrees of "biodilution" of the available Hg (Jernelöv et al. 1975) can be ruled out as an important factor in explaining the variations in the Hg content of the plankton, as there is no evidence of a significant connection between Hg concentration (Table 1) and biological productivity (Jackson 1988b, table 8). There is indeed a negative correlation between Hg levels in >10 μm plankton and the mean primary productivity of the sampling region for the period 18 June to 17 August 1981, but it is very insignificant ($r = -0.642$; $P >> 0.1$). Hg in >73 μm plankton gave comparable but even more insignificant results ($r = -0.312$; $P >> 0.1$).

The observation that the Hg data for >73 μm plankton, in contrast with >10 μm plankton, form two separate and divergent curves when plotted against the organic content of the sediment — one for Southern Indian Lake and Granville Lake combined and another one characterized by a lower slope and higher Hg levels per unit concentration of organic matter for Notigi Reservoir lakes (Fig. 3) — has interesting implications from the standpoint of food-chain effects. The fact that Hg data for >73 μm plankton from main-stream and backwater environ-

TABLE 2. Correlation matrix relating the Hg content of >10 μm and >73 μm plankton to the Hg chemistry of the associated water and sediment. — = data not computed because not relevant.

	Hg in plankton							
	June				August			
	>10 μm		>73 μm		>10 μm		>73 μm	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Total Hg in June 1981 sediment	−0.573	>>0.1	−0.427	>>0.1	−0.457	>>0.1	−0.482	>>0.1
Total Hg in Aug. 1981 sediment	−0.748	>>0.1	−0.995	>0.001, <0.01	−0.380	>>0.1	−0.205	>>0.1
Total Hg in Aug. 1983 sediment	−0.558	>>0.1	0.332	>>0.1	0.966	>0.001, <0.01	−0.449	>>0.1
CH_3Hg^+ in June 1981 sediment	−0.407	>>0.1	0.280	>>0.1	0.786	>0.05, <0.1	0.791	>0.1
CH_3Hg^+ in Aug. 1983 sediment	−0.217	>>0.1	0.332	>>0.1	0.945	>0.001, <0.01	0.517	>0.1
Total organic Hg in Aug. 1981 sediment[a]	—	—	—	—	0.912	>0.02, <0.05	0.956	>0.02, <0.05
Hg methylating capability of Aug. 1983 sediment[a]	−0.561	>>0.1	0.245	>>0.1	0.929	>0.001, <0.01	−0.399	>>0.1
$CaCl_2$-extractable Hg in June 1981 sediment[a]	−0.782	>0.1	0.135	>>0.1	—	—	—	—
$CaCl_2$-extractable Hg in Aug. 1981 sediment[a]	—	—	—	—	0.337	>>0.1	0.830	>0.1
$CaCl_2$-extractable Hg (Aug. 1981) × Hg methylating capability (Aug. 1983)[a]	—	—	—	—	0.900	>0.02, <0.05	0.745	>>0.1
Total Hg in June 1981 water	0.0642	>>0.1	−0.440	>>0.1	—	—	—	—
CH_3Hg^+ in June 1981 water	−0.340	>>0.1	0.179	>>0.1	—	—	—	—
CH_3Hg^+ in Aug. 1981 water	—	—	—	—	−0.589	>>0.1	0.714	>0.1
Total Hg in June 1981 suspended matter	−0.986	>0.001, <0.01	−0.707	>0.1	—	—	—	—
Total Hg in Aug. 1981 suspended matter	—	—	—	—	0.807	>0.05, <0.1	0.460	>>0.1
Suspended Hg in June 1981 water	−0.883	>0.02, <0.05	−0.509	>>0.1	—	—	—	—
Suspended Hg in Aug. 1981 water	—	—	—	—	0.392	>>0.1	−0.288	>>0.1

[a]See Jackson (1988b).

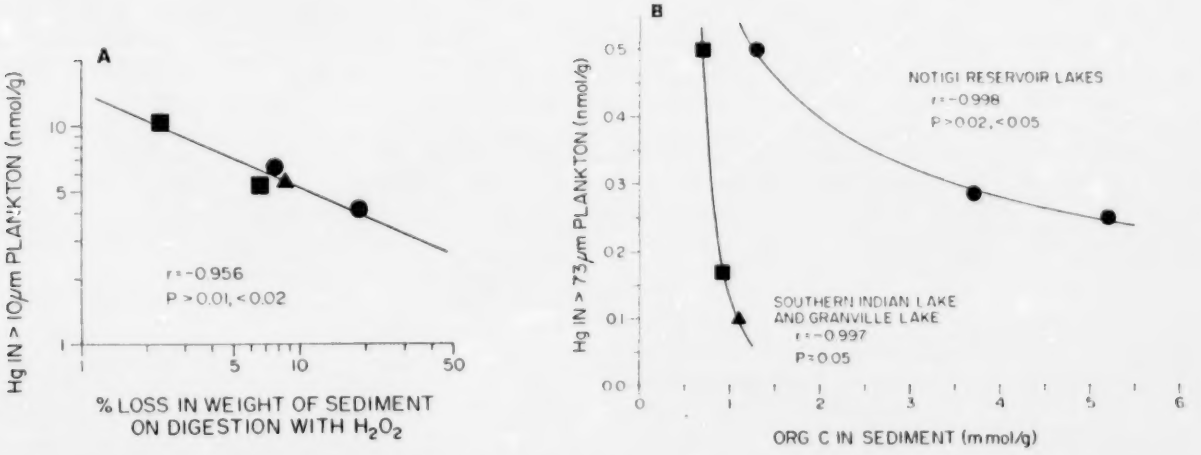

FIG. 3. Relationships between Hg in plankton collected in June 1981 and organic matter in associated bottom sediments. (A) Hg in >10 μm plankton plotted against the sediment's percent loss in weight on digestion with H_2O_2 and (B) Hg in >73 μm plankton plotted against the organic C content of the sediment. ▲, Granville Lake; ■, Southern Indian Lake; ●, Notigi Reservoir lakes.

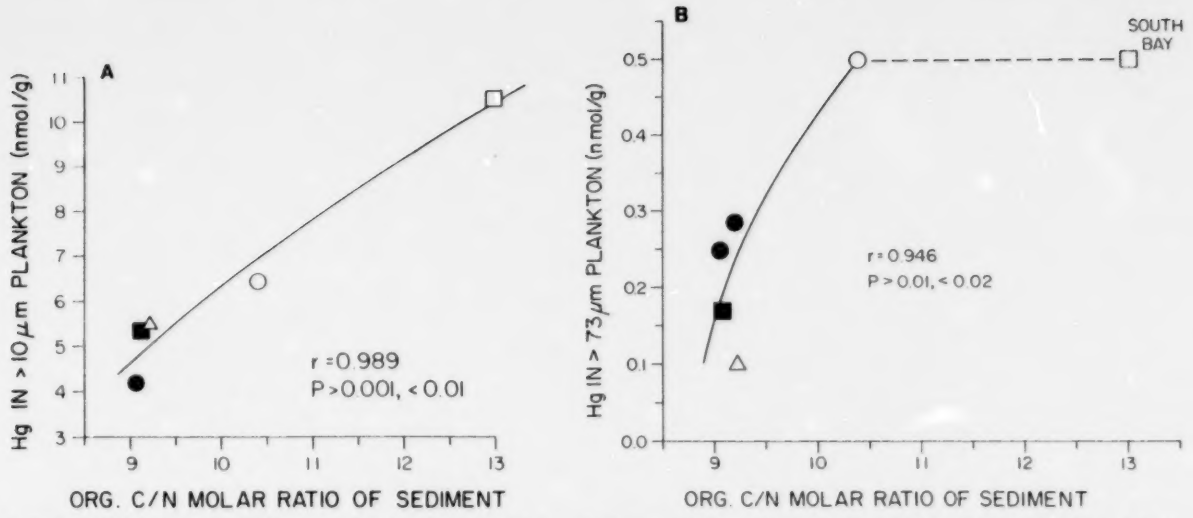

FIG. 4. Relationships between the Hg concentrations in (A) >10 μm plankton and (B) >73 μm plankton collected in June 1981 and the organic C/N ratio of the associated sediment. In Fig. 4B the regression curve represents all sampling sites except South Bay; the broken line signifies the levelling off of the curve. Explanation of symbols same as in Fig. 1. Data for >73 μm plankton from Bodaly et al. (1987).

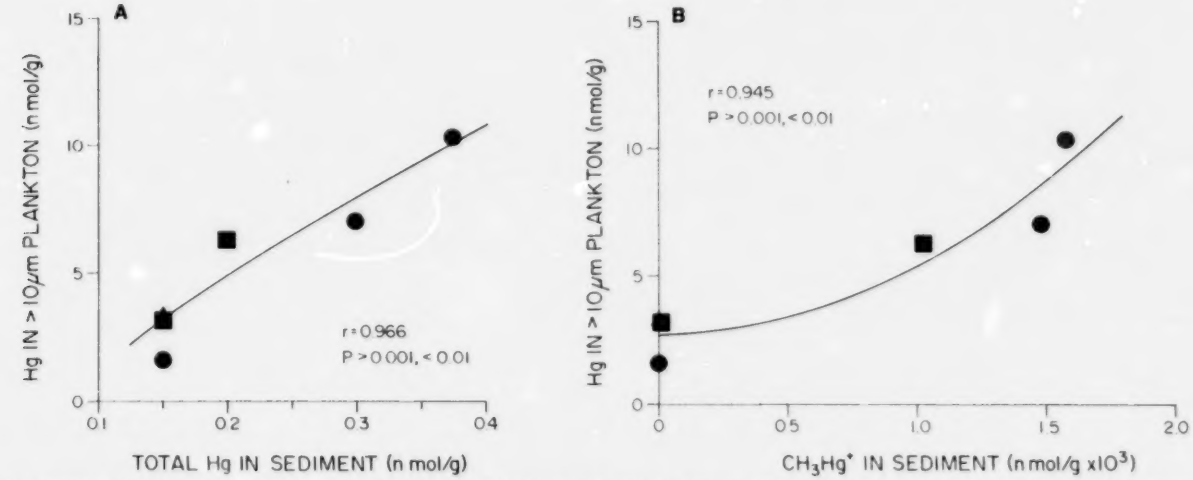

FIG. 5. Relationships between the Hg content of >10 μm plankton collected in August 1981 and the (A) total Hg and (B) CH_3Hg^+ content of bottom sediments sampled in August 1983. Explanation of symbols same as in Fig. 3.

ments are less sharply differentiated from each other than is the case with >10 μm plankton (Table 1) is also significant in this regard.

Comparison of the results obtained for >10 μm plankton (Fig. 1, 2, 3A, 4A), >73 μm plankton (Fig. 3B, 4B), and fish (McGregor 1980; Bodaly et al. 1984, 1987; Jackson 1987) provides indirect evidence that the proportion of CH_3Hg^+ to nonmethyl Hg in the aquatic organisms of northern Manitoba increases progressively up the food chain, as in other freshwater ecosystems mentioned in the literature (D'Itri 1972; Huckabee et al. 1979). At the lower end of the food chain is the phytoplankton, the dominant element of the >10 μm plankton, whose Hg content is entirely unrelated to the distribution of CH_3Hg^+ or the rate of CH_3Hg^+ production in the environment, and is therefore unrelated to effects of impoundment, but apparently depends on the bioavailability of Hg as determined by Hg-binding substances and environmental factors such as current action and aeration. At the opposite extreme, at the upper end of the food chain, are piscivorous fish such as walleye and northern pike, whose Hg levels are mainly determined by the abundance of CH_3Hg^+ and rate of CH_3Hg^+ production in the environment and therefore increase with increasing extent of postimpoundment flooding (in the order Granville Lake < Southern Indian Lake < Notigi Reservoir lakes) (Bodaly et al. 1984; Jackson 1987, 1988b) but are independent of the factors that regulate Hg uptake by phytoplankton. Zooplankton (>73 μm plankton) occupies an intermediate position in the food chain and is consequently intermediate with respect to the factors influencing the bioaccumulation of Hg (Fig. 3B). Food chain effects and accumulation of Hg by fish will be more fully treated elsewhere (T. A. Jackson, in preparation).

To summarize, the analytical data are consistent with the following conclusions: (1) the forms of Hg assimilated by the plankton are mostly inorganic (nonmethyl); (2) the availability of this Hg to the plankton is depressed when the Hg is bound by particulate organic matter and sulfides and is enhanced when

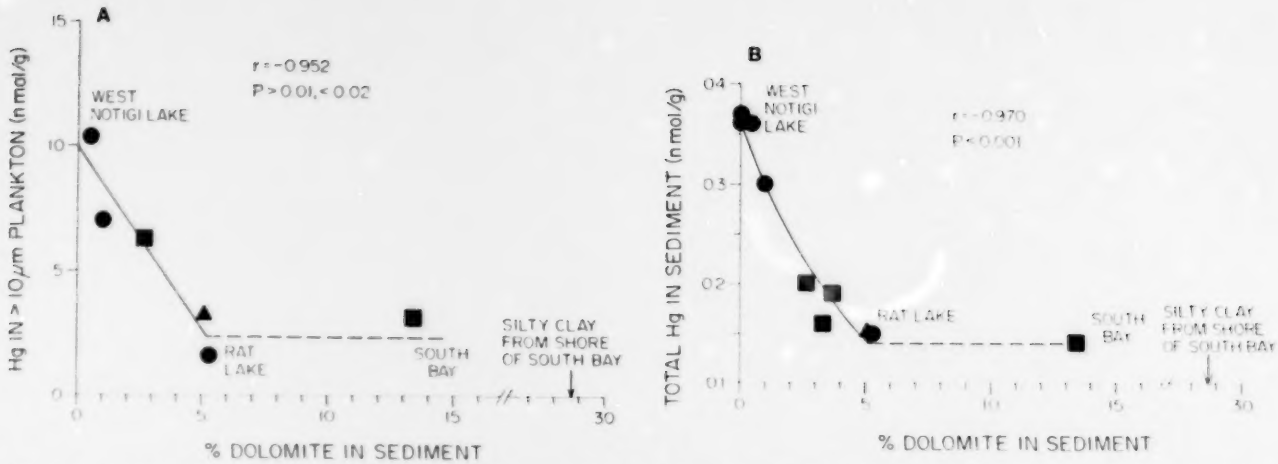

FIG. 6. Hg content of (A) >10 μm plankton collected in August 1981 and (B) sediment collected in August 1983 plotted against the abundance of dolomite in the sediment. Regression lines represent all sampling sites except South Bay; the broken lines signify levelling off of the curves. Explanation of symbols same as in Fig. 3.

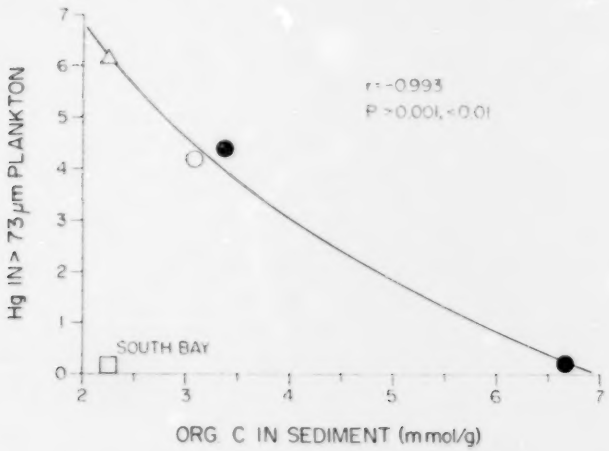

FIG. 7. Relationship between the Hg content of >73 μm plankton collected in August 1981 and the organic C content of bottom sediment sampled in August 1983. Regression curve represents all sampling sites except South Bay. Explanation of symbols same as in Fig. 1.

the Hg-binding substances are decomposed; (3) Hg availability is therefore greatest in mainstream regions, where vigorous flushing and aeration promote rapid decomposition of Hg-binding substances and release of the bound Hg; and (4) the proportion of CH_3Hg^+ to inorganic Hg is greater in >73 μm plankton than in >10 μm plankton owing to accumulation of CH_3Hg^+ up the food chain.

Plankton sampled in August

The Hg content of >10 μm plankton collected in August showed a radically different pattern of variation than the Hg content of plankton collected in June (Table 1). Hg concentrations in August plankton gave strong positive correlations ($0.01 > P > 0.001$) with the "total" (HNO_3/HCl-extractable) Hg and CH_3Hg^+ concentrations of sediments collected in August 1983 (Fig. 5A, 5B; Table 2) and with the sediment's Hg methylating capability (Table 2), and a weaker but nonetheless significant positive correlation ($0.05 > P > 0.02$) with the "total organic Hg" content of sediment collected in August 1981 (Table 2). Thus, in August, in contrast with June, the accumulation of Hg by >10 μm plankton appeared to depend simply on the total supply of inorganic Hg or CH_3Hg^+ in the environment. Again, biomass dilution seems not to have been a factor: Hg levels in the plankton gave a significant positive correlation with primary productivity measured over the interval 18 June to 17 August 1981 ($r = 0.989$; $N = 4$; $0.02 > P > 0.01$) whereas biomass dilution would have produced an inverse relationship.

Hg levels in August samples of >10 μm plankton did not correlate significantly with total Hg or CH_3Hg^+ concentrations in sediments collected in 1981 (Table 2), even though they correlated strongly with the total Hg and CH_3Hg^+ content of sediment samples collected in 1983. This probably indicates that the 1983 sediment samples happened to be more representative of those areas of the sediment–water interface which had the greatest influence on the transfer of Hg from sediments to plankton after the onset of summer stratification. At four of the six sampling regions for which August plankton data are available, the sediments were collected at shallower sites in 1983 than in 1981, and at only one site was the water deeper (Jackson 1988b, table 1). This suggests that in the midsummer, when the lakes were more or less stratified, the immediate source of the Hg taken up by phytoplankton was relatively shallow, yet fine-grained, bottom sediment in contact with the epilimnion (the habitat of the phytoplankton); the deeper sediments in the hypolimnion were probably isolated owing to stratification of the water column.

Hg levels in the >10 μm August plankton generally tended to increase with the extent of postimpoundment flooding; thus, they were highest in Notigi Lake and were relatively low in Southern Indian Lake and Granville Lake (the "control" lake). Rat Lake, however, was anomalous: although the second greatest postimpoundment rise in lake level occurred in Rat Lake, the Rat Lake plankton had the lowest Hg concentration, and the values for Rat Lake, South Bay, and Granville Lake all clustered close together at the lower end of the observed range of Hg levels. Moreover, Hg concentrations in plankton were lower in South Bay than in Long Bay, even though the rise in lake level was the same in both.

These observations appear to reflect a general tendency of flooding to release bioavailable Hg into the water, the tendency

TABLE 3. Hg content of benthic chironomids, oligochaetes, nematodes, and pelecypods collected in June 1981. Except where otherwise noted, all chironomids were larvae. $\bar{X}$ = mean; N = no. of replicate samples; n.d. = no data.

Sampling site	Hg concentration (nmol/g fresh wt.)			
	Chironomids	Oligochaetes	Nematodes	Pelecypods
Southern Indian Lake				
Long Bay (shallow cove)	1.04	3.48	2.29	1.53
South Bay	0.578	n.d.	0.546	0.115
Notigi Reservoir				
Rat Lake	0.107[a]	0.213	0.482	0.391
Central Mynarski Lake	0.0987[b]	1.68	0.816	0.0770
Notigi Lake (east basin)	0.118	0.255	0.160	0.402
	0.129[c]			

[a] $\bar{X}$ = 0.107; range = 0.0897–0.141; N = 4.
[b] $\bar{X}$ = 0.0987; range = 0.0718–0.1[illegible]; N = 3.
[c] Hg content of pupae.

TABLE 4. Correlation matrix relating the Hg content of benthic invertebrates to the Hg chemistry of the associated sediment.

	Hg in benthic organisms							
	Chironomids		Oligochaetes		Nematodes		Pelecypods	
	r	P	r	P	r	P	r	P
CH_3Hg^+ in June 1981 sediment	−0.780	>0.1	−0.785	>0.1	−0.794	>0.1	−0.388	>>0.1
Total Hg in June 1981 sediment	−0.629	>>0.1	0.301	>>0.1	−0.136	>>0.1	−0.355	>>0.1
$CaCl_2$-extractable Hg in June 1981 sediment[a]	−0.789	>0.1	−0.565	>>0.1	−0.299	>>0.1	−0.347	>>0.1
Hg methylating capability of Aug. 1983 sediment[a]	−0.287	>>0.1	0.876	>0.1	0.462	>>0.1	0.374	>>0.1

[a] See Jackson (1988b).

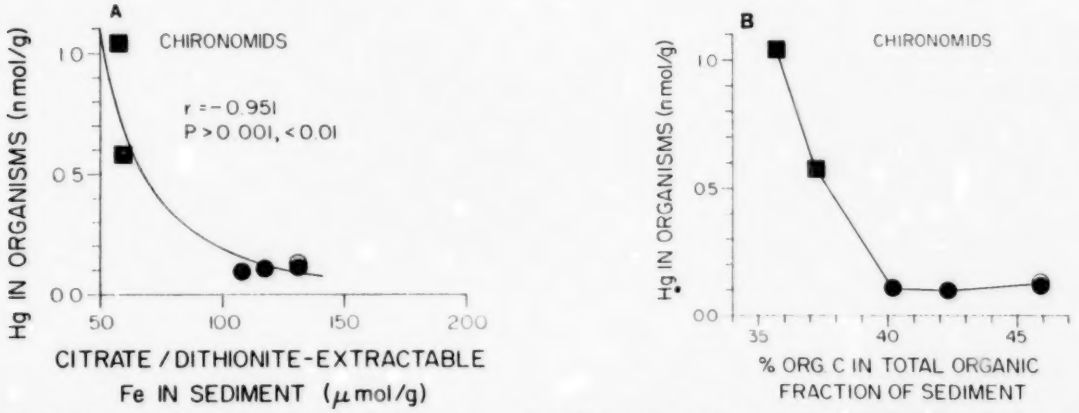

FIG. 8. Relationships between the Hg content of chironomid larvae (solid symbols) and pupae (open symbol) and (A) the citrate/dithionite-extractable Fe content of associated bottom sediment and (B) the percentage of organic C in the total organic fraction of the sediment. ■, Southern Indian Lake; ● and ○, Notigi Reservoir lakes. In the plot shown in Fig. 8B, $r = -0.841$; $0.05 > P > 0.02$.

being to some extent obscured, however, by effects of local conditions. The low Hg values for Rat Lake and South Bay probably indicate that the biological uptake of Hg was impeded by suspended clay and silt. South Bay has an anomalously great abundance of suspended fine-grained mineral detritus owing to erosion of shoreline deposits of Pleistocene glaciolacustrine silty clay, and Rat Lake is the receiving basin for turbid water flowing out of South Bay (Newbury et al. 1984; Jackson 1988b). The suspended clay and silt may interfere with the bioaccumulation of Hg by scavenging and immobilizing dissolved Hg species in the water, thereby making them less available for biological uptake, and by inhibiting microbial methylation of Hg in the sediments (not only by adsorbing Hg but also by diluting and burying organic nutrient substrates); there is also evidence that this material actively promotes demethylation of CH_3Hg^+ (Jackson 1987, 1988a, 1988b). Furthermore, the clay and silt, being poor in Hg compared with most of the lake muds in the region (compare Hecky et al. 1987 (table 2 and "Errata") and Jackson 1988b (table 9)), probably dilute and rapidly bury the more Hg-rich particulate matter being deposited on the bot-

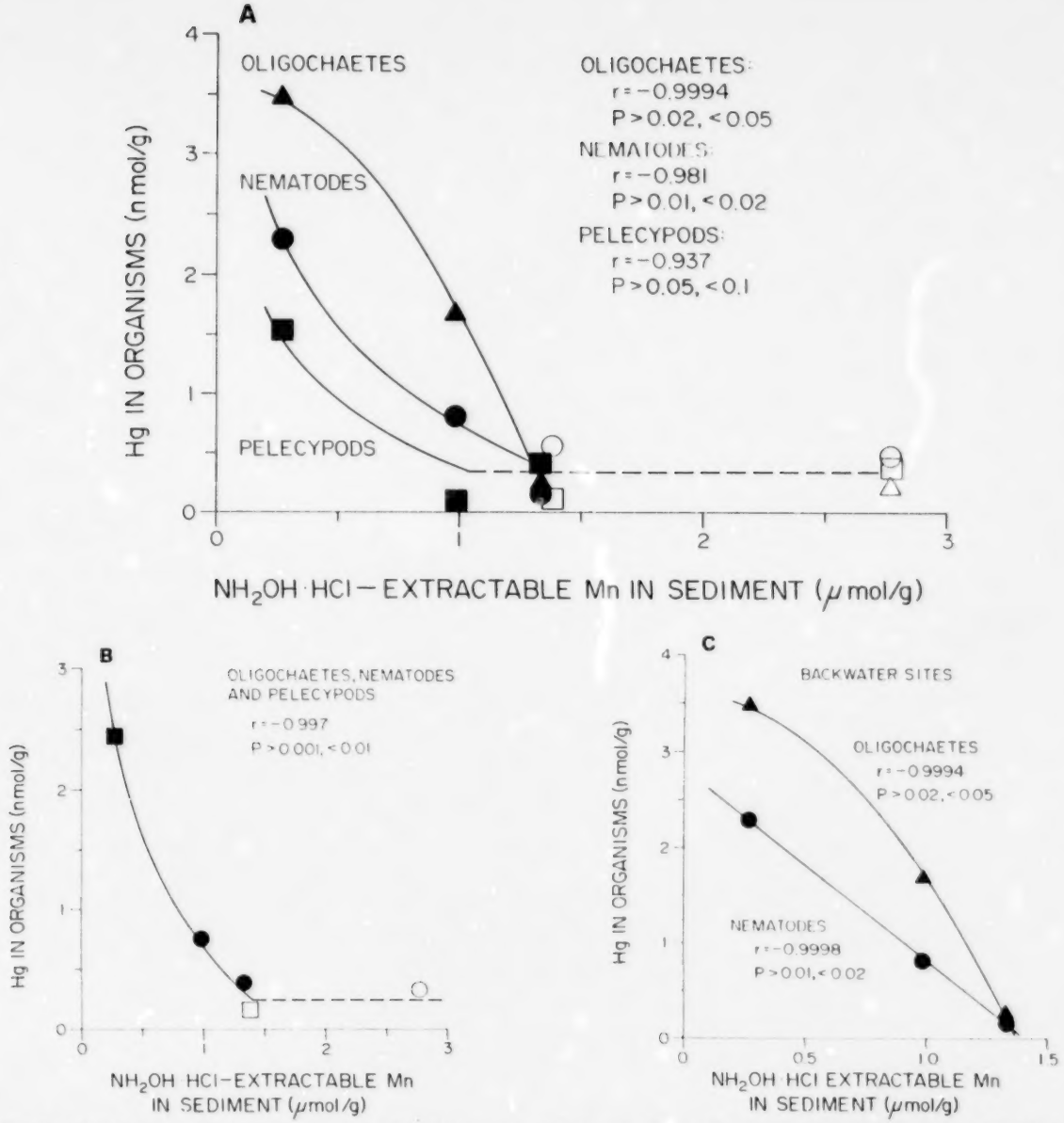

FIG. 9. Relationships between Hg concentrations in oligochaetes, nematodes, and pelecypods and the $NH_2OH{\cdot}HCl$-extractable Mn content of the associated bottom sediment. (A) Individual plots for oligochaetes (▲,△), nematodes (●, ○), and pelecypods (■, □) from all sites; solid symbols, backwater sites; open symbols, mainstream sites. (B) Plot employing weighted average Hg concentration of combined oligochaetes, nematodes, and pelecypods from each site; ■, □, Southern Indian Lake; ●, ○, Notigi Reservoir lakes; solid symbols, backwater sites; open symbols, mainstream sites. (C) Plots for oligochaetes (▲) and nematodes (●) in backwater sites. Regression analyses and curves in Fig. 9A and 9B represent all sampling sites except Rat Lake, which is represented by the symbols on the far right. Broken lines connecting the symbols for Rat Lake with the regression curves indicate levelling off of the curves at higher Mn concentrations.

tom, thereby hindering the release of Hg from the sediments to the water column.

The hypothesis that clay and silt eroded from shoreline deposits interfere with the uptake of Hg by plankton is strongly supported by Fig. 6A and 6B, which demonstrate that the Hg concentrations in >10 μm plankton and bottom sediment are inversely related to the dolomite content of the sediment. Dolomite is a major component of the Pleistocene silty clay deposits in the field area and is unlikely to have been derived from any other source; therefore, it is an excellent marker mineral for tracing eroded, redeposited Pleistocene glacial or glaciolacustrine sediment in the rivers and lakes of the region (Jackson 1988b). The anomalously high concentration of eroded silty clay in South Bay is clearly shown in Fig. 6. (The only other anomaly is an aberrantly high concentration of Hg with respect to dolomite in sediment from East Mynarski Lake (Jackson 1988b, tables 5, 9). Compared with the other lakes in the study area, East Mynarski Lake also has an anomalously high level of primary productivity and anomalously high concentrations of sulfide in its sediments (Jackson 1988b). In view of the

TABLE 5. Correlation matrix relating the Hg content of benthic invertebrates and different physicochemical characteristics of their environment to the depth of water at the sampling site. The environmental variables represent all sampling regions except Granville Lake and the west basin of Notigi Lake (see text). All data represent samples collected in June 1981.

	Depth of water	
	r	*P*
Hg in chironomids	−0.940	>0.01, <0.02
Hg in oligochaetes	−0.919	>0.05, <0.1
Hg in nematodes	−0.811	>0.05, <0.1
Hg in pelecypods	−0.531	>>0.1
Temperature of water at bottom	−0.968	>0.001, <0.01
Citrate/dithionite-extractable Fe in sediment	0.987	<0.001
%C in total organic fraction of sediment	0.978	<0.001
NH_2OH·HCl-extractable Mn in sediment	0.588	>>0.1

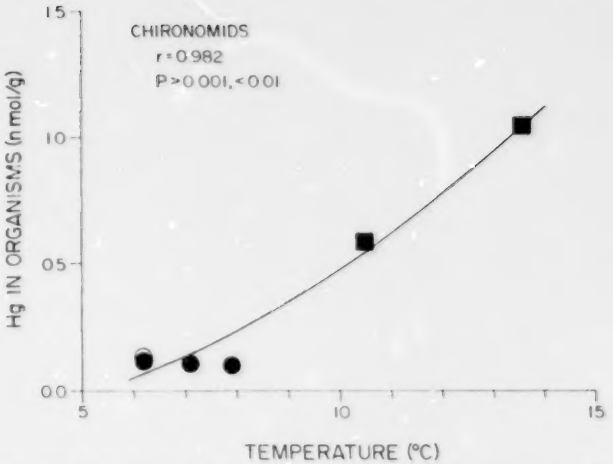

FIG. 10. Relationship between the Hg content of chironomids and the temperature of the bottom water in June 1981. Explanation of symbols same as in Fig. 8.

strong tendency of organic matter and sulfide to bind and accumulate Hg, the relatively large concentration of Hg in the sediment of East Mynarski Lake is undoubtedly a result of the high rate at which organic matter and sulfide accumulate in that particular lake.)

As with the >10 μm plankton, the geographical pattern of variation in the Hg levels of the >73 μm plankton was radically different in August than in June, although the >10 μm and >73 μm plankton fractions collected in August differed greatly from each other. The Hg concentrations in all but one of the >73 μm zooplankton samples collected in August gave a strong inverse correlation with the organic C content of the sediment (Fig. 7). Virtually the same results were obtained when Hg in plankton was plotted against the organic C content of whole or centrifuged surface water. The aberrant sampling site was South Bay, where the Hg concentration in plankton was anomalously low. The most Hg-rich plankton samples came from Granville Lake, which has not been affected by hydroelectric development, whereas the plankton from Central Mynarski Lake, where impoundment caused a 6.9-m rise in lake level, had the second lowest Hg concentration.

The negative correlation between Hg in zooplankton and organic C in sediments and water can be ascribed to reduced bioavailability of Hg resulting from the binding of dissolved Hg by humic matter and other organic complexing agents. Note that the highest organic C concentrations in sediments and the lowest Hg levels in zooplankton occurred in backwater regions, where autochthonous humic matter leached from local forest soils and muskeg is most highly concentrated. The aberrantly low Hg content of South Bay zooplankton can probably be explained by suppression of the bioaccumulation of Hg due to the anomalously great abundance of eroded shoreline clay and silt at that particular site.

The marked seasonal differences between the geographical variations in the Hg content of plankton in the lakes of the study area cannot be explained without additional information, but the most likely reason would seem to be seasonal changes in the physical conditions in the water column. In June, when the spring flood was in progress, there was relatively vigorous flushing by river currents and therefore diminished influence of local environmental conditions. In August, when river flow had slackened, local conditions probably had a much stronger effect on the plankton.

Benthic Invertebrates

As with plankton other than the >10 μm plankton collected in August, Hg levels in benthic chironomids, oligochaetes, nematodes, and pelecypods were not significantly related to Hg levels and methylation rates in their immediate surroundings (Tables 3, 4). Hg concentrations in all four types of benthic invertebrate consistently gave highly insignificant correlations ($P > 0.1$) with the CH_3Hg^+, total Hg, and $CaCl_2$-extractable Hg concentrations of the sediment and with the Hg methylating capability of the sediment, and 75% of the correlation coefficients were negative (Table 4).

Surprisingly, the highest Hg concentrations in benthic invertebrates occurred in Southern Indian Lake rather than Notigi Reservoir lakes (Table 3) whereas the distribution of total Hg, CH_3Hg^+, and "available inorganic Hg" concentrations and relative rates of Hg methylation in the bottom sediments (not counting aberrantly low total Hg levels in samples collected from the west basin of Notigi Lake in 1981 (Jackson 1988b)) would lead one to expect the reverse of that result. Furthermore, Hg data for different invertebrate taxa differed systematically among themselves, both in absolute value and in their geographical distribution. These findings imply that the net rates of Hg accumulation by benthic invertebrates were more strongly influenced by certain environmental and biological processes than by the abundance of the CH_3Hg^+ or inorganic Hg species in their habitat. As discussed below, the concentrations of Hg in the organisms appear to be determined largely by the composition of the sediment, although ambient temperature may also play a role. Specific biological factors such as feeding habits must be taken into account as well.

Hg levels in benthic animals correlated inversely with the concentrations of hydrated Fe and Mn oxides and C-rich humic matter in the bottom sediment. The Hg content of chironomids decreased logarithmically with increasing concentrations of citrate/dithionite-extractable Fe in the sediments (Fig. 8A) and with increasing abundance of C in the organic fraction of the sediment (Fig. 8B), levelling off at higher Fe and organic C concentrations. These variables are highly dependent on the

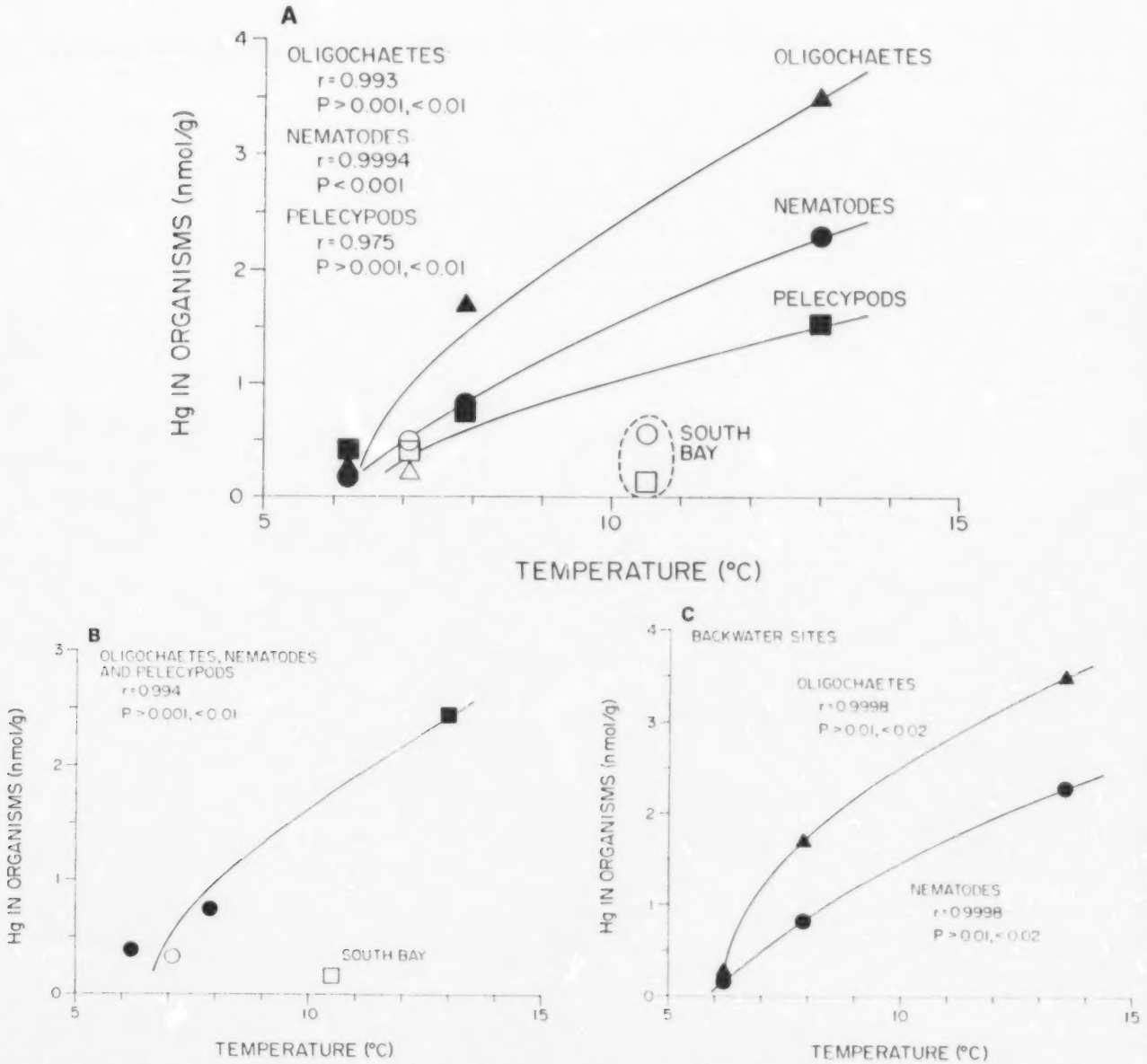

FIG. 11. Relationships between Hg concentrations in oligochaetes, nematodes, and pelecypods and the temperature of the bottom water. (A) Individual plots for oligochaetes, nematodes, and pelecypods from all sites. (B) Plot employing weighted average Hg concentration of combined oligochaetes, nematodes, and pelecypods from each site. (C) Plots for oligochaetes and nematodes in backwater sites. Regression analyses and curves in Fig. 11A and 11B represent all sampling sites except South Bay. Explanation of symbols same as in Fig. 9.

depth of water, the abundance of Fe oxide and C increasing with depth while the Hg concentrations in chironomids decrease (Table 5). (*Note*: The relationship between the Hg content of the organisms and the nature of the sedimentary organic matter has also been commented upon by W. F. Warwick (unpubl. data).)

In contrast with the Hg content of chironomids, the Hg concentrations in oligochaetes, nematodes, and pelecypods varied inversely with the $NH_2OH{\cdot}HCl$-extractable Mn content of the sediment, levelling off sharply at Mn concentrations greater than about 1.3 μmol/g (Fig. 9A, 9B). Also note that the correlation of these variables with depth of water is relatively weak (Table 5). Furthermore, there is a clear-cut separation between the Mn-rich mainstream regions and the Mn-poor backwater regions, the significant correlation between Hg and Mn being confined to the backwater zone (Fig. 9A). In the more Mn-rich environments, in which the Hg levels in the organisms were minimal, the three types of invertebrates differed only slightly in Hg content; but in Mn-poor environments, where Hg levels were high, they differed considerably, the Hg levels decreasing in the order oligochaetes > nematodes > pelecypods (Fig. 9A, 9C). In Fig. 9A the regression curves for nematodes and pelecypods are similar in shape but differ markedly from the curve for oligochaetes, suggesting that the Hg uptake kinetics are different in oligochaetes than in the other organisms.

TABLE 6. Estimates of total biomass of benthic macroinvertebrates at different sampling sites (computed from data supplied by W. F. Warwick (pers. comm. and unpubl. data)).

Sampling site	Total biomass (g/m²)
Southern Indian Lake	
Long Bay (shallow cove)	1.504
South Bay	6.092
Notigi Reservoir	
Rat Lake	52.894
Central Mynarski Lake	42.520
Notigi Lake (east basin)	7.513

TABLE 7. Correlation matrix relating Hg concentrations in different benthic invertebrate groups to the total biomass of the benthic macroinvertebrate community.

	Total biomass of macroinvertebrate community	
	r	P
Hg in chironomids	−0.872	>0.05, <0.1
Hg in oligochaetes	−0.674	>>0.1
Hg in nematodes	−0.618	>>0.1
Hg in pelecypods	−0.720	>>0.1

The systematic differences between oligochaetes, nematodes, and pelecypods may reflect differences in feeding habits. An oligochaete typically passes huge quantities of mud through its gut when feeding (Clegg 1974; Pennak 1978), and this probably results in rapid assimilation of available forms of Hg from ingested sediment particles. In contrast, nematodes as a whole have a wide range of feeding habits and feed on a variety of living and nonliving organic materials, only some of which are scavenged from bottom sediments (Crofton 1966; Pennak 1978), while pelecypods are filter feeders which consume suspended organic particles from the water column and even winnow inedible sediment particles out of their food (Clegg 1974; Pennak 1978). Thus, the intake of bottom sediment by the organisms, like the concentrations of Hg in their bodies, presumably diminished in the order oligochaetes > nematodes > pelecypods, suggesting a correlation between the quantity of fine-grained sediment consumed and the amount of Hg assimilated in a given period of time. Such a correlation would be a natural consequence of the fact that the finer-grained bottom sediments are enriched in Hg with respect to the overlying water (Jackson 1988b, tables 9, 10). On the other hand, a cautionary note would be appropriate: the Hg data for oligochaetes, nematodes, and pelecypods are subject to an unknown degree of error because (1) the gut contents could not be voided prior to chemical analysis and (2) the weights of the pelecypod specimens included the shell weights.

The extractable sedimentary Fe and Mn fractions which correlate inversely with Hg levels in benthic invertebrates are thought to represent collodial hydrated oxides, here symbolized as FeOOH and MnOOH (see references in Jackson 1988b, table 2). However, the FeOOH was associated with sedimentary humic matter as represented by brown organic substances extracted with 0.1 M NaOH. Thus, the citrate/dithionite-extractable Fe gave strong positive correlations with the colour (absorbance at 465 nm) of NaOH extracts of the sediments (for June samples, $r = 0.967$; $P < 0.001$) and with NaOH-extractable organic C (for June samples, $r = 0.926$; $P < 0.001$) (see data in Jackson 1988b, tables 7, 13). The FeOOH was probably complexed with humic substances, which have a strong affinity for hydrated ferric oxides and Fe(III) in general (Schnitzer and Khan 1972). The percentage of C in the organic matter is interpreted as an approximate measure of the proportion of allochthonous (land-derived) humic matter in the organic fraction of the sediment. This interpretation is based on the following facts:

(1) The %C values for the organic matter in sediments collected in June (with the exception of samples from Granville Lake and the west basin of Notigi Lake) gave significant positive correlations with the concentrations of NaOH-extractable colour ($r = 0.962$; $0.01 > P > 0.001$) and NaOH-extractable organic C ($r = 0.894$; $0.02 > P > 0.01$) in the sediments. (Granville Lake and west Notigi Lake sediments, which had aberrantly low values of %C and had a number of other anomalies in common (Jackson 1988b), gave a separate but parallel trend. Possibly the reason for the anomaly is that the sampling regions in Granville Lake and west Notigi Lake, being located in zones of exceptionally vigorous fluvial current action, had relatively low concentrations of humic matter derived from local soils and muskeg, and thus had proportionately larger amounts of riverborne humic matter transported from further upstream.) Coloured organic substances extracted from sediment or soil with alkali consist principally of humic matter, and the colour intensity and C content of the extract tend to increase with both the concentration of humic matter in solution *and* the humic matter's degree of humification, or maturity (degree of "humic" as opposed to "fulvic" character) (Schnitzer and Khan 1972).

(2) Allochthonous humic matter formed from remains of land plants and other terrestrial organisms generally tends to be more mature, and hence more C rich, than is autochthonous humic matter derived from aquatic organisms (Jackson 1975).

(3) In northern Manitoba the sediments from the backwater zone of Notigi Reservoir, where the influence of local drainage from highly humic forest soil and muskeg is particularly great (see data in Jackson 1988b, tables 4, 11), had the most C-rich organic matter. (However, the meaning of this relationship is ambiguous because the %C values were also strongly correlated with depth of water, the depth being greater at the Notigi Reservoir sites than at the Southern Indian Lake sites (Table 5).)

The relationships illustrated in Fig. 8 and 9 suggest that the binding of Hg species by FeOOH and MnOOH, and possibly by higher molecular weight humic substances, reduces the availability of Hg to benthic animals, thereby limiting their rate of Hg accumulation. It has been demonstrated that hydrated oxides and organic matter may interfere with the accumulation of heavy metals by freshwater molluscs (Tessier et al. 1984) and rainbow trout fry (*Salmo gairdneri*) (T. A. Jackson, unpubl. data and manuscr. in preparation), and the same principles could very well apply in the present case. Morever, higher molecular weight humic fractions of sediments bind Hg preferentially with respect to lower molecular weight fractions (Jackson et al. 1980).

This provisional interpretation of the results shown in Fig. 8 and 9 implies that chironomids accumulate certain chemical species of Hg more readily than do the oligochaetes, nematodes, and pelecypods and that these Hg species are also preferentially adsorbed by FeOOH or humic acid, or FeOOH–humic complexes, whereas the other three invertebrate groups preferentially accumulate other forms of Hg that happen to be preferentially adsorbed by MnOOH. Although further research is

needed to confirm it, this hypothesis is reasonable because of the following considerations: (1) the Hg accumulated by invertebrates, unlike Hg in fish tissue, commonly has a high proportion of nonmethyl, or inorganic, Hg (Huckabee et al. 1979; Windom and Kendall 1979; T. A. Jackson, unpubl. data and manuscr. in preparation), which could comprise a variety of chemical species, such as soluble complexes, that differ in their affinities for adsorption sites on sedimentary particles and in their availability for uptake by organisms; and (2) hydrated Fe and Mn oxides in Mn nodules are known to have different trace-metal preferences (Burns and Fuerstenau 1966; Calvert and Price 1977) and therefore could conceivably discriminate between different chemical species of Hg.

Ambient temperature may also have influenced the accumulation of Hg by the benthic invertebrates. Thus, Hg levels in chironomids and oligochaetes gave strong positive correlations with water temperature at or near the sediment–water interface (Fig. 10, 11A). Hg concentrations in nematodes and pelecypods, however, gave relatively weak positive correlations with temperature because the specimens from South Bay were anomalously low in Hg with respect to temperature; strong correlations were obtained only if the data for South Bay were disregarded (Fig. 11A, 11B). Actually, the plot for oligochaetes is not strictly comparable with the plots for nematodes, pelecypods, and chironomids because no oligochaetes were found in South Bay. Nevertheless, the previously discussed biogeochemical kinship between oligochaetes, nematodes, and pelecypods as contrasted with chironomids (Fig. 8A, 8B, 9A) is sufficient grounds for surmising that if a complete set of Hg data were available for oligochaetes, they would show essentially the same pattern of variation as the data for nematodes and pelecypods.

At backwater sites, oligochaetes were consistently richer in Hg than were nematodes (Fig. 11C), as discussed above, and their respective regression lines diverge with increasing temperature, although the correlation coefficients and significance probabilities for the two curves are identical. The Hg levels in backwater faunas correlate as strongly with temperature as with $NH_2OH{\cdot}HCl$-extractable Mn or even more strongly; however, in the plots of Hg against temperature (Fig. 11), unlike the plots of Hg against $NH_2OH{\cdot}HCl$-extractable Mn (Fig. 9), there seems to be no logical basis for treating backwater and mainstream samples as separate subgroups.

As the results illustrated in Fig. 10 and 11 demonstrate, a direct effect of temperature on the uptake of Hg by invertebrates is a distinct possibility. From a physiological standpoint this is plausible, as other studies have established that rates of Hg bioaccumulation in at least some aquatic organisms increase with temperature owing to enhancement of metabolic rates (MacLeod and Pessah 1972; Burkett 1974; Shin and Krenkel 1976). The aberrantly low Hg levels in organisms from South Bay (Fig. 11A, 11B) could be attributed to diminished bioavailability of Hg due to the scavenging of Hg by the massive quantities of clay and silt being introduced into the bay as a result of shoreline erosion (cf. Fig. 4B, 6A, 6B, 7). On the other hand, this aberration did not occur in the chironomid data (Fig. 10).

A third interpretation of the data for benthic invertebrates has been proposed by W. F. Warwick (unpubl. data and pers. comm.). Noting that the total invertebrate biomass (mass of organisms per unit area of lake bottom) tended to be greater in Notigi Reservoir lakes than in Southern Indian Lake (Table 6), Warwick postulated that the paradoxical occurrence of low Hg levels in the Notigi Reservoir fauna and high Hg levels in the Southern Indian Lake faunas resulted from biodilution of the Hg (cf. Jernelöv et al. 1975). This hypothesis, however, does not stand up well under scrutiny. Regression analysis relating the Hg concentrations in the organisms to the total biomass of the macroinvertebrate community at each site yielded negative correlation coefficients as predicted by the biodilution theory, but all four of the correlations are insignificant (Table 7). (Besides, at least a small part of each correlation is attributable to self-correlation.) Thus, biodilution appears to play only a very trifling role, if any.

The question now arises whether the observed variations in the Hg concentrations in benthic invertebrates can be better explained by the distribution of hydrated oxides and humic matter in the sediment or by variations in ambient temperature. Both interpretations are plausible, and, as they are not mutually exclusive, both could well be correct; but further research, including controlled experiments as well as field studies, would be needed to disentangle the cause-and-effect relationships. The data for chironomids are particularly ambiguous, as they are all strongly dependent on depth of water and therefore correlate significantly with each other.

Nevertheless, it would seem that the suggested inhibitory effect of FeOOH, MnOOH, and humic matter on the biological uptake of Hg can best account for the available data as a whole. In the graph relating Hg levels in nematodes and pelecypods to ambient temperature, the data for South Bay are definitely aberrant (Fig. 11A) whereas no such anomaly exists in the plots of Hg level against $NH_2OH{\cdot}HCl$-extractable Mn. This favours the idea that adsorption of Hg by MnOOH was the principal limiting factor controlling the rate at which the organisms accumulated Hg. Another argument in favour of this hypothesis arises from the relationships between the Hg concentrations in the organisms and the depth of water at the sampling sites (Table 5). Pelecypods gave by far the poorest correlation (the only highly insignificant relationship ($P >> 0.1$)) and pelecypods are also the only organisms among the four groups investigated which specialize in filter feeding and actively exclude sediment particles. All three other groups either specialize in deposit feeding or include deposit-feeding species. This pattern of variation suggests that the depth-related factor which controlled the uptake of Hg by the animals was the nature of the ingested sediment — for instance, the abundance of FeOOH, MnOOH, and humic matter — not the temperature.

Acknowledgments

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